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16. ABSTRACT

Most plant diseases consist of delicate interactions between higher plants and microorganisms. Acidic precipitation represents an environmental stress that has been shown to affect expected development of some diseases and similar phenomena under experimental conditions. From the perspective of the "disease triangle" framework, this impact may be expressed through increased plant susceptibility, decreased plant susceptibility through altered metabolic pathways, decreased pathogen activity or increased pathogenicity. Aerial plant parts are directly exposed to rainfall and the potential influence of acidic precipitation on pathogen and diseases of aboveground tissues seems obvious. However, soilborne pathogens and root diseases may also be significantly altered by short-term acidification of the soil solution resulting from acid deposition, or by gradual changes in bulk soil chemical characteristics over a long period of time. Although research in this area is only beginning, knowledge of the biological, ecological and economic impacts of diseases of agricultural crops and native vegetation suggests that acidic precipitation plays a significant role in the subtle interactions of plants and their parasites.

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CHAPTER 3

Effects of Acid Precipitation on Plant Diseases

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The chemistry of rain in much of the eastern United States has been modified to such an extent that levels of acidity considered insufficient to induce acute botanical effects may indeed significantly influence the epidemiology of numerous plant diseases. The role of acid rain on the subtle balance between host and parasite life cycles has been and continues to be a subject of scientific investigation. Evidence to date suggests that acid precipitation may significantly alter host-parasite interactions and hence modify otherwise predictable disease responses. Although the majority of available data were gathered under greenhouse or field "simulated rain" conditions, we present experimental evidence that addresses potential effects of acid rain on plant disease.

Many definitions for the concept of "disease" in plants have been proposed over a period of decades [1], but none is completely satisfactory to all. Like most "definitions" in the biological sciences, problems arise with the gray areas of those situations. Some would insist that the altered physiological processes induced by acid precipitation itself constitute bona fide "disease," and we would be hard-pressed to argue effectively against such a claim. However, to keep this chapter in its proper context with other topics in this volume, our concept of disease will be limited to processes in plants typified by injurious physiological activity induced by biotic pathogens (fungi, bacteria, nematodes, parasitic seed plants, mycoplasmas, spiroplasmas, rickettsias, protozoans, viruses and viroids) over a period of time. This idea can be presented in the form of the familiar "disease triangle" (Figure 1), which indicates that disease is a function of the simultaneous occurrence of a susceptible host plant, a virulent parasitic organism and environmental conditions conducive to their interaction over time. This environmental component is as important to disease development as the host or parasite. Without favorable environmental conditions, the disease process will not occur.

Acid precipitation represents an alteration in the environment component

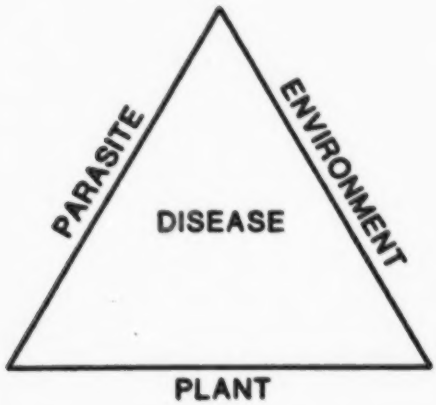

Figure 1. Disease triangle. Disease (as presented in this chapter) is a function of a physiological interaction between a plant host and a parasite in an environment conducive to that interaction, over a period of time. Acid precipitation represents a factor in the "environment" component. The amount of disease, in terms of incidence or severity, is reflected in the size of the triangle.

(represented by a star in Figures 2 and 3). Hypothetically, it could have three effects on a disease situation. First, within the range of acidity currently occurring in precipitation, no change may be evident. Either the perturbation is simply not sufficient to alter the otherwise predictable course of the host–parasite interaction, or it produces a balance of conflicting effects. Second, acid rain may influence host resistance, pathogen virulence or pathogen inoculum density in such a way as to increase disease incidence or severity on a plant or within a plant population (Figure 2). Third, acid precipitation may decrease plant susceptibility, parasite virulence or parasite inoculum such that the disease process is decreased in severity or incidence (Figure 3). Presumably, the ultimate effect will vary with the host–parasite situation under consideration, the range of rainfall acidity involved and the impact of acidity on each of the myriad phases of the host–parasite interaction.

The literature addressing this specific topic is scant. However, knowledge of the biology of plants, their parasites and the interactions of these populations in the environment can suggest ways in which acid rain might influence plant diseases. This type of speculation is valuable in directing research efforts into these topics, and we offer some of these hypotheses here.

This chapter is divided into two broad sections: (1) effects of acid rain on airborne plant diseases and foliar and stem pathogens; and (2) effects on root

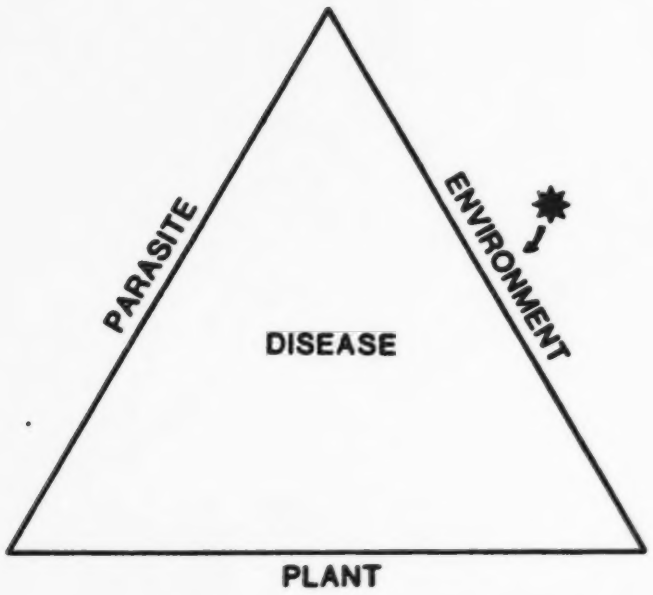

Figure 2. Acid precipitation (*) in the environment may influence some plant–parasite interactions in a manner that results in an increase in disease incidence or severity.

Figure 3. Acid precipitation (*) may influence some plant–parasite interactions such that overall disease incidence or severity is decreased.

diseases and soilborne pathogens. Hypothetical influences on beneficial root–microorganism symbioses will be mentioned briefly. Using the disease triangle as a guide, the effects of acidic precipitation on diseases will be approached through the perspective of plant-mediated and parasite-mediated effects.

EFFECTS OF ACIDIC PRECIPITATION ON FOLIAR AND STEM DISEASES AND ON FOLIAR-STEM PATHOGENS

Plant-Mediated Effects

Recent research has addressed direct effects of acid rain on the deterioration of plant tissue. Literature exists on the role of the cuticle, epicuticular waxes and the epidermis as barriers to penetration by foliar plant pathogens [2]. Presumably, when acid rain erodes leaf surfaces and kills tissue, the consequences for the microecology of leaf surfaces may be great. Changes in the leaf surface environment could favor or inhibit ingress by pathogenic microorganisms.

Researchers have speculated on the possible significance of direct weathering of leaf surfaces by acid rain, and such weathering may directly or indirectly influence plant—parasite interactions. Rain, and indeed, acid rain, is probably the most significant environmental factor influencing the weathering of plant tissue [3,4]. Martin and Juniper [4] observed that weathered leaf surfaces exhibited increased surface wettability, often a critical factor in pathogen propagule survival and ingress. They also noted that weathered surfaces may pose a weaker barrier to direct penetration of pathogens. However, weathered leaf surfaces may aid in retention of pesticides due to the erosion of hydrophilic epicuticular waxes that would otherwise shed residues [5].

Plant stress and wounds accelerate senescence of plant tissue. Infection by an entire group of plant pathogens, i.e., the facultative parasites, is favored by senescent tissue. Hence, the incidence and severity of plant diseases induced by many of the ascomycetous and basidiomycetous fungi that are placed in this category may be increased. Conversely, populations of obligate parasites, i.e., some oomycete fungi, rust fungi, powdery mildews and viruses that require healthy tissue for infection may be significantly reduced by acid rain stress on plants. For example, Bruck et al. [6] observed that when loblolly pine (*Pinus taeda* L.) seedlings were exposed twice before and after inoculation with basidiospores of *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* (the fusiform rust pathogen) to episodes of acid rain at pH 5.6, 4.0, 3.2 and 2.4, needle necrosis ranged from 0% at pH 5.6 to 60% at pH 2.4. Six months following inoculation they noted significantly fewer rust galls among trees previously exposed to lower-pH rains. Basidiospore penetration takes place through healthy tissue of the needle or fascicle junction. Induction of tissue necrosis by acidified rains would reduce the potential target area; hence, fewer galls would be expressed (the result of lower infection rates).

Diseases caused by fungi that act as facultative saprophytes would be expected to develop differently from those induced by obligate parasites. Numerous fungi that cause tree cankers, i.e., *Nectria* spp., *Hypoxylon* spp., *Eutypella* spp. and others, require wounds to gain ingress. Preliminary reports [7] indicate that the increased acidification of rains in the northeastern United States may correlate with observed increases in stem cankers. It is difficult to separate these observations

om the effects of other environmental perturbations, but the correlations warrant rther investigation.

Stapp [8] notes that most bacterial plant pathogens gain ingress into plants ia wounds and natural openings. Microscopic wounds induced by low-pH rains iay act as courts for bacterial infection. Shriner [9] exposed bean leaves to simulated ains of pH 3.2 or 6.0 and noted a marked increase in the incidence and severity of lesions formed by the bacterial pathogen *Pseudomonas phaseolicola* (Burkh.) Dows at the lower pH. Since simulated acid rain clearly induces plant wounding, Shriner's hypothesis that simulated rains induced numerous small necrotic lesions, resulting in an increase in bacterial pathogenesis, seems to be supported.

Acid rain may have both detrimental and beneficial effects on host plant physiology with respect to response to foliar plant pathogens [9]. Acid precipitation may disturb otherwise normal carbon and nutrient metabolism; hence, defense mechanisms may be altered. However, plants have evolved highly efficient anatomical and biochemical processes to respond to both environmental perturbation and pathogen ingress [10]. The ability of a plant to defend or repair itself depends on the availability and allocation of resources. Acid rain can directly deprive a plant of necessary resources via foliar and soil leaching of nutrients and exudates, or it may indirectly shift the physiological balance of resources from defense to repair of injured tissue.

Many plants react to injury (as may occur in episodes of acid rain) by "shifting" metabolism into defensive-related pathways. Hypersensitive reactions that "trap" obligate parasites within dying tissues have been observed in numerous instances, such as in certain viral diseases and some rusts. Compartmentalization of fungal invasion in trees by the mobilization of antibiotic compounds has been documented. Bruck et al. [6] reported a significant increase in anatomical "resistant traits" in loblolly pine seedlings exposed to low-pH rain treatments both before and after inoculation with the fusiform rust pathogen. They speculate that the acidified rain insult may, by itself or in concert with fungal invasion, induce the host plants to contain or halt the process of *Cronartium* pathogenesis. The incidence of abnormally small galls was greater when the pH of simulated rains was lowered. Low pH also correlated to an increase in reaction zones (possibly accumulations of phenolics), galls with rough exfoliative bark tissue (correlated to field resistance) and infection sites with no gall symptom expression.

The potential ramifications of these plant-mediated effects of acidified rain to plant disease epidemiology are many. Pathogen propagules not only may apparently be killed or rendered nonviable, but they may also be contained following initial infection and colonization of plant tissue by the effects of acid rain. Data collected as of this writing suggest that rains of high acidity may significantly alter otherwise predictable plant-mediated disease responses in nature.

Parasite-Mediated Effects

Plant pathogens may directly be altered or destroyed by the effects of acid rain. Numerous species of fungi and bacteria are disseminated via wind-blown or splashed

rain. The ability of many bacteria to survive in an acidified environment is poor [11]. In addition, Leben [12] observed severe growth reduction in 15 species of plant pathogenic fungi grown on media acidified to pH 3.2. Shriner [13] found that the acidity of water in which *Pseudomonas phaseolicola* bacterial inocula were disseminated onto bean greatly influenced both the bacterial population and infectivity. At pH 3.2, bacteria that remained in the infection droplets were incapable of infecting either healthy leaves or foliage injured by acid rain.

Lacy et al. [14] studied the effects of simulated acidified precipitation on populations of the bacteria *Erwinia herbicola* (Lohnis) Dye and *Pseudomonas syringae* V. Hall. They observed that no colony-forming units of these epiphytic bacteria were recovered on agar plates after exposure for 50 min to acidified water at pH 2.0 and that there was a significant depression of bacterial populations at pH 3.0, as compared to bacteria exposed to pH 4.0, 5.0, 6.0 or 7.0.

Bruck et al. [6] hypothesized that fusiform rust basidiospore inocula exposed to episodes of simulated acid rain following inoculation to loblolly pine may have been reduced in its infectivity. Highly significant differences in the number of galls initiated were noted among trees exposed before and after inoculation with the rust fungus. The authors postulated that the reduction of galls at low-pH exposures may have been due to the reduction of viable propagules available to initiate the infections. The probability of successful pathogen ingress would most probably be reduced as fewer viable propagules would initiate infections.

EFFECTS OF ACID RAIN ON ROOT DISEASES AND SOILBORNE PATHOGENS

Acid precipitation may affect diseases caused by soilborne pathogens by mechanisms similar to those influencing foliar diseases, i.e., in plant- or pathogen-mediated ways. Many of these mechanisms may be induced through acute effects of short-term acidification of soil water. In addition, the potential for long-term effects on both mechanisms due to chronic exposures is of possible significance.

Plant-Mediated Effects

Like other phases of plant growth and development, optimum seed germination occurs within a certain pH range. For example, Teigen [15] demonstrated that the greatest percent seed germination of Norway spruce seeds occurred at pH 4.8. Lower germination percentages were observed in soils drenched with dilute sulfuric acid or amended with lime. Furthermore, at pH 3.8, 80% of the seedlings that did emerge were not "normal." Exact response, whether positive or negative, of germinating seedlings to simulated acid rain is species-specific [16]. Plants for which early emergence and establishment are delayed are often susceptible to attack by damping-off pathogens over a longer period of time and thus have increased chances of being killed. Exposure of seeds germinating near the soil surface to

acid solutions entering the soil as rainwater might induce such delays in emergence and early development.

Simulated acid rains can induce direct damage to plant foliage and, as discussed previously, such acute damage to tissues can alter plant susceptibility to pathogen attack. Root tissue is known to be sensitive to acidic solutions as well. Cohen et al. [17] noted significant reductions in root fresh and dry weights for carrot plants exposed throughout the growing season to simulated rain acidified with sulfuric acid to pH 4.0 or below, compared with yields for plants exposed to pH 5.6 treatments. Yields (fresh and dry weights) of beet roots were reduced by pH 3.0 exposures. Arnon and Johnson [18] demonstrated that lettuce and tomato plant roots turned gray, lost turgor and collapsed when exposed to nutrient solutions adjusted to pH 3.0. Similar effects by low-pH rain on roots near the soil surface could lead to the presence of senescent tissue that might provide infection courts for facultative parasites in soil. Such an effect may have been observed by Roman and Raynal [16], who applied acidified nutrient solutions to sugar maple seedlings. After four days of constant exposure, many of the radicles treated with pH 2.4 and 3.0 solutions darkened and softened at the tip. When these seedlings were planted in greenhouse soil and watered with tap water, only 7 and 53% of the seedlings (at pH 2.4 and 3.0, respectively) survived. However, if exposed seedlings from these treatments were planted in soil and watered with distilled water containing fungicide, all seedlings from all treatments survived.

The occurrence of foliage exposure to acid rain has implications for root diseases as well as foliar diseases. Many conditions that affect aboveground plant parts modify quantities and compositions of root exudates, which in turn cause changes in the biology of the rhizosphere [19]. McGuirt [20] exposed soybean plants three times per week for 40 days to simulated rains of pH 6.0 or 3.5. Assays performed on rhizosphere soils with a range of nutrient agar media indicated that rhizospheres of plants exposed to "rains" of pH 3.5 selected for bacteria that grew quickly on media amended with vitamins, amino acids and other complex nutrients. Apparently, roots of plants exposed to the more acidic treatments exuded more of these complex growth factors. These results are consistent with data reviewed by Moore [21], which indicate that exposure of plant roots to low-pH conditions increases permeability of cell membranes and allows increased leakage of cell contents.

Changes in root exudates resulting from exposure to acid rain would alter microorganism interrelationships involving potential pathogens in the rhizosphere or might alter pathogen responses to the presence of plant roots. Such situations may influence disease occurrence. For example, the charcoal root rot pathogen *Macrophomina phaseolina* (Tassi) Goid. has a host range of more than 400 plant species, and sclerotium populations have been correlated with populations of certain actinomycetes and bacteria in soil [22]. Changes in rhizosphere species composition could decrease or stimulate pathogen antagonists and affect disease incidence accordingly. Marx and Bryan [23] found that sporulation of *Phytophthora cinnamomi* Rands and infection patterns in pine roots depended on qualitative characteristics of rhizosphere bacterial populations.

Chemotactic responses of pathogen spore germ tubes depend on root exudate composition as well [24]. Yung and Hickman [25] have demonstrated that the cationic fraction of pea root exudates caused accumulation of *Pythium aphanidermatum* (Edson) Fitzp. zoospores as well as the crude exudates. Zentmyer [26] demonstrated the relationship among foliage, root exudates and responses by motile spores when he removed plant foliage and found reduced attraction for pathogen zoospores by the roots and fewer infections. Necrosis of foliar tissue due to acid rain or abscission of damaged leaves might produce a similar effect.

Chronic effects of repeated exposures of plants to acid rain could conceivably affect root diseases through nutrient imbalance induced in the host. Nutrient status in plant tissues often plays a role in disease development. Yellowing of pin oak foliage due to iron deficiency is common when the soil pH is >7 and iron becomes unavailable for root uptake. Such nutrient availabilities are among the factors that determine the optimum soil pH ranges for various plant species [27], and plants under nutrient stress are frequently more susceptible to attack by pests of various kinds. Changes in tissue nutrient status might occur due to leaching of minerals from foliage, soil or both, resulting in changes of host–parasite relations. For example, increased calcium concentrations in tomato tissues can lead to increased resistance to vascular wilt caused by the soilborne fungus *Fusarium oxysporum* Schlect. emend. Snyd. and Hans [28]. Mineral deficiencies in *Pinus resinosa* Ait. seedlings apparently contributed to heavy losses due to damping-off by *Fusarium* spp. [29]. Various minerals have been shown to leach from plant tissues and soils exposed to simulated acid rain [30–34]. Effects of acid rain on plant diseases through soil nutrient availability and soil pH changes might become apparent only after years of exposure to long-term crops on mineral soils, i.e., forest trees, due to current rates of acid inputs and buffering capacities of most soils [35].

Parasite-Mediated Effects

Direct effects of acid rain on soilborne plant pathogens could conceivably alter the progress of plant–parasite interactions. Populations of most root pathogens are greatest within 10–15 cm of the soil surface, where they have great impact on feeder roots of established plants and the limited root systems of young seedlings. Indeed, since most seeds germinate within a centimeter or so of the soil surface, pathogens quite near the surface are of extreme importance in the pathology of young plants. It is also in this zone that soil microorganisms are under the greatest influence of rainwater chemistry. Acidic rainwater percolating through the soil profile changes in chemical characteristics through exchange phenomena in soil, but (depending on soil physical and chemical characteristics) varying soil depths may be required to significantly alter severely acid rain. Near-surface pathogens may thus be influenced in some soils.

The optimum growth and reproduction of a soil microorganism occurs within a defined pH range that is species-specific, which may determine incidence of a given disease. For example, the actinomycete *Streptomyces scabies* (Thaxt.) Waks.

and Henrici is sensitive to acid conditions in vitro, and this probably explains the rare occurrence of potato scab in soils characterized by pH less than 5.4 [36]. Club root of cabbage (caused by *Plasmodiophora brassicae* Wor.), however, is severe in some acid soils and is rare in alkaline soils, probably because the spores of the pathogen germinate poorly when the pH is >7 [37]. Activities of these and other pathogens may be greatly affected when acid water enters the soil. A sudden influx of a pH 3.5 soil solution may halt the infection process by *S. scabies*, for example. Rainwater of this acidity occurs presently in the eastern United States.

Different phases of soilborne plant pathogen life cycles respond differently under different pH conditions. Cameron and Milbrath [38] found that most of the eight *Phytophthora* spp. tested grew best at in vitro pH levels of 4.5–5.5. Chee and Newhook [39] observed that the low pH levels in pH-adjusted soil extracts that would inhibit production of *P. cinnamomi* sporangia probably would also limit plant growth. However, Pegg [40] found fewer sporangia and a lower incidence of pathogen isolation when sulfur was used to adjust infested soil to pH 3.8. A drop in pH from 5.0 to 4.5 caused only an 8% reduction in *P. cinnamomi* chlamydospore germination [41], but the same pH reduction caused a 94% depression of mycelial growth after 28 days [38]. Thus, the phase during which an acid rain event occurs may determine the nature of the ultimate effect on disease.

Some of the relationships between plant roots and motile zoospores of oomycete fungi were briefly mentioned previously. Khew and Zentmyer [42] suggest that tropic responses of zoospores are related to cationic charges in the soil solution surrounding the root. A sudden influx of acidic rainwater might impair normal tropic responses of zoospores to charged substances. If tropic responses of pathogen motile spores are indeed related to cationic charges, the sudden influx of acidic rainwater into the soil might alter normal tactic functions of the pathogen. Allen and Harvey [43] described "negative chemotaxis" of *P. cinnamomi* zoospores exposed to different concentrations of HCl or its salts. Zoospores exhibited abnormal turning movements, movement away from diffusing solutions and encystment. Experiments demonstrated that the response depended on critical concentrations of cations rather than on concentration gradients. For hydronium ions, the critical concentration was estimated at 37 μM.

Effects on various stages of pathogen life cycles could eventually influence their populations in soil. Lawry [44] studied fungal populations in soils of sites exposed to acid runoff from strip mines and found net decreases in fungal species diversities. Shafer et al. [45] filled columns to different depths with fir nursery soil naturally infested with *Phytophthora cinnamomi*. After five consecutive daily exposures to simulated rains (pH 5.6, 4.0, 3.2 or 2.4), average *P. cinnamomi* populations in the columns and the pH of effluent water from the columns varied directly with rain treatment pH and soil depth. Propagules within 4 cm of the soil surface had less chance of survival of exposures to rains of pH 4.0 or less than did propagules at greater depths. In another study, Shafer (unpublished results) found that populations of viable *Macrophomina phaseolina* sclerotia in the top 4 cm of pine nursery soil in pots were 20% lower in soils exposed 25 times over 86 days to simulated rains at pH 2.4 than at pH 3.2, 4.0 or 5.6.

Several reports suggest that many plant-parasitic nematodes frequently occur in slightly acidic soils (pH 5.0–6.0 range). Growth and reproduction by several species seem to decrease as bulk soil pH exceeds 6.0. Growth and reproduction of many species apparently are inhibited beyond the pH 4.0–7.0 range [46]. Data related to nematodes are based on overall soil pH; the effect of mass flow of acidic rainwater in soil on nematodes should receive experimentation. To date, only Shriner [47] has examined the impact of acid rain on a nematode-induced plant disease. In a field study with root-knot of kidney beans, he found that plants exposed to simulated rain of pH 3.2 had only 34% as many *Meloidogyne hapla* Chitwood eggs per root system and 48% fewer root galls, compared to plants exposed to pH 6.0 treatments. Plant size and yield, as well as soil pH, were the same for both groups of plants. Shriner speculated that the free-living larval stages of the nematode may have been affected by short-term acidification of soil water, or that parasitism and reproduction of adult females within the plant roots were inhibited by physiological alterations in the host induced by acid rain treatments.

Effects on Beneficial Root–Microorganism Relationships

Some soilborne microorganisms form beneficial symbioses with plant roots. Although these are not "disease" relationships in the eyes of most plant pathologists, these situations share certain characteristics with their harmful counterparts, such as infection and tissue colonization.

Perhaps the best known of these mutualistic symbioses is the infection and nodulation of legume roots by species of the bacterium genus *Rhizobium.* This relationship allows fixation of atmospheric dinitrogen gas by the root–bacterium system. Effects of acid rain on legume nodules have been the subject of several studies. Shriner [47] found that kidney beans and soybeans exposed over eight weeks in the field or five weeks in the greenhouse to simulated rains of pH 3.2 developed an average of 75% fewer nodules than plants exposed to pH 6 treatments. Overall, 74% of the plants that failed to nodulate at all had received pH 3.2 treatments. Results differed between plants that had either foliage only or soil only exposed, suggesting that at least part of the effect was host-mediated. Plants with fewer nodules exhibited lower nitrogenase activity. In a time-related study, nodulation was inhibited most by daily exposures to pH 3.2 treatments applied 15–21 days after plants were inoculated with *Rhizobium.* Waldron [48] also found inhibited nodulation of soybean and kidney bean plants by simulated rains of pH 3.2, but nitrogenase activity was similar to that of plants exposed to deionized water "rains," suggesting some type of compensatory effect by the plant–bacterium system. Waldron also demonstrated that hydrogen ions rather than sulfate ions were responsible for treatment differences, and that soil drenches were more inhibitory than foliar applications, further suggesting a host-mediated effect.

Mycorrhizae are perhaps the most common plant root–soil microorganism

symbiosis in nature. Gerdemann [49] states that, "In nature, the mycorrhizal condition is the rule, the nonmycorrhizal condition, the exception." The various patterns of fungal infections of plant roots characteristic of different mycorrhizal types benefit their host plants by effectively increasing absorptive surface areas of the root system and providing for increased uptake of certain soil minerals (and in some cases, water). Presumably, the fungi involved might respond in ways similar to fungal pathogens to acid water in soil. Feicht [50] planted soybeans into pots containing soil infested with the endomycorrhizal fungus *Glomus macrocarpus* Tul. and Tul. var. *geosporus* (Gerd. and Nichol.) Trappe and Gerd. Plants were exposed in the field to simulated rains over the pH range 2.8–5.5 twice each week for 15 weeks. No changes were observed for *G. macrocarpus* colonization of roots. However, sporulation of the fungus associated with plants exposed to pH 2.8 treatments was inhibited by approximately 40%, compared to plants exposed to pH 5.6 treatments.

Ectomycorrhizae of certain forest tree species have been demonstrated to protect the plants from root diseases by several mechanisms [51]. Effectiveness of several of these, such as provision of a physical barrier to parasite infection and activity of antibiotics, might be reduced by acid rain through physiological effects on the host or by acid water in the soil. For example, damage to the fungal mantle might allow pathogens to breach this protective barrier, or antibiotics produced by the endophyte could be inactivated by low pH conditions.

CONCLUSIONS

Most plant diseases consist of delicate interactions between higher plants and microorganisms. Acidic precipitation represents an environmental stress that has been shown to affect expected development of some diseases and similar phenomena under experimental conditions. From the perspective of the "disease triangle" framework, this impact may be expressed through increased plant susceptibility (through physical wounding or impaired physiological activity), decreased plant susceptibility through altered metabolic pathways, decreased pathogen activity (from intolerance to low-pH conditions by vegetative or survival structures, or from increased activity of competitors) or increased pathogenicity (by stimulation from more favorable pH conditions for acidophilic organisms, or by elimination of competitors). Aerial plant parts are directly exposed to rainfall and the potential influence of acidic precipitation on pathogen and diseases of aboveground tissues seems obvious. However, soilborne pathogens and root diseases may also be significantly altered by short-term acidification of the soil solution resulting from acid deposition, or by gradual changes in bulk soil chemical characteristics over a long period of time. Although research in this area is only beginning, knowledge of the biological, ecological and economic impacts of diseases of agricultural crops and native vegetation suggests that acidic precipitation plays a significant role in the subtle interactions of plants and their parasites.

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